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A century of progress in the natural sciences, 1853-1953.

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Page(s): Page 747, Page 748, Page 749, Page 750, Page 751, Page 752, Page 753, Page 754, Page 755, Page 756, Page 757, Page 758, Page 759, Page 760, Page 761, Page 762, Page 763, Page 764, Page 765

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PLANT GEOGRAPHY

By RONALD GOOD
University College, Hull, Yorkshire

So INTIMATELY is the history of man related to the distribution of plants that it is scarcely an exaggeration to suggest that the study of plant geography must have begun with the first dawnings of man's consciousness of the potentialities of his environment, but today most botanists are content to claim for it a history of more comprehensible length. Some date its beginning from the days of Tournefort, who flourished about 1700 and to whom is attributed the first recognition of latitudinal and altitudinal zonation and the way in which these are the reflection of one another. Others call attention to Linnaeus' classification of plant habitats—his *Stationes Plantarum*—in the *Amoenitates.* The commonest practice, however, is to regard von Humboldt, the great German naturalist, as the father of plant geography. His travels in South America in the opening years of the nineteenth century resulted in one of the first scientific descriptions of equatorial vegetation, and the recognition of his fundamental contribution (von Humboldt, 1817). Humboldt has the merit of emphasizing that the first chapter of this science was, as it has been in so many others, essentially one of exploration and description.

In another sense, also, von Humboldt is a notable landmark. He is the connecting link between the great voyages of geographical exploration in the latter half of the eighteenth century, among which those of Captain Cook are so prominent, and the series of great scientific expeditions which may be considered to have begun with the voyage of the *Beagle* from 1831 to 1836. In view of the great distinction of Charles Darwin's subsequent studies in botany one cannot but regret, on reading his account of this voyage, that he was not then more concerned with plants. His preoccupation at that time with geology and zoology, an emphasis which later had such profound consequences, is evident, and it was not until a few years later, when the young Joseph Hooker set out in the *Erebus* on a voyage lasting from 1839 to 1843, that a real botanical milestone was reached.

It is not easy now to realize that these two series of expeditions—the great voyages of geographical adventure on the one hand and the great scientific explorations initiated by the voyage of the *Beagle* on the other—were in fact separated by little more than half a century for they seem to belong to different ages. True, these years had been memorable ones and had witnessed the vast liberating forces of which the American War of Independence and the French Revolution were expressions, yet even this does not adequately account for the difference of outlook that distinguished the second quarter of the nineteenth century from the third quarter of the eighteenth. It seems clear enough that there must have been in the latter period a tremendous intellectual leaven at work which was destined in the space of a comparatively few years to lighten the whole body of biological thought. This leaven may be described as the growing consciousness, not yet expressed in words but evidently present in the minds of many people, that the uninspiring doctrines of biological immutability must soon give way to something more in tune with the spirit of the times and, it may be added, more in accord with a rapidly growing body of observed facts. The spark that ultimately fired this tamped charge was, of course, the appearance of Darwin's *The Origin of Species* in 1859, but it is easy to see now not only that the fuse had been smouldering for years, but that the study of plant geography had made no small contribution to this result.

Indeed, it may be said with truth that, from the point of view of this subject, the foundation of the California Academy of Sciences in 1853 could scarcely have been at a more auspicious time, for it was followed within the short space of seven years by a series of publications which became classic and which, together, raised the subject of plant geography to a position of special importance and significance. First came Hooker's essay on the New Zealand flora (1853), to be followed two years later by A. L. P. P. de Candolle's *Géographie Botanique Raisonnée* (1855), which still remains one of the most considerable of all such works. Then, almost together, came Asa Gray's study of the flora of Japan (1859), the *Origin* itself (1859), and Hooker's second essay, on the flora of Tasmania (1859).

Looking back now in the light of so much after-knowledge it is difficult to recapture the intellectual atmosphere of the earlier eighteen-fifties, when the scientific world was so much smaller than it is now. Such recapture is particularly difficult when based on much of the contemporary literature. De Candolle's book is an instance of this. Here is a closely packed study of his subject of more than a thousand pages, of which the headings might serve almost equally well for a survey of similar scope today and in which the author comments with judgment on almost every aspect of the subject, and yet it is written entirely in what can today only be called the restricted idiom of pre-evolution. Even mutability is admitted, and there are discussed, more than once, the changes which species may come to suffer with the passage of time. But there the curtain falls, and one may search in vain for any recognition of the possibility that what may in due course befall species may itself be the origin of others. It is a remarkable example of scientific thought restrained by dogma.

De Candolle's book is in many ways a striking example of one written years before its time. It not only discusses many subjects the potentialities of which are really only now being tested, such as the order of families in floras or the proportions between monocotyledons and dicotyledons, but, as has been said, it discusses the circumstances surrounding the hypothetical creation of species with considerable acumen. So much emphasis is placed on this aspect of his subject that one almost inevitably wonders whether the author's major premise, which is the supernatural creation of species, can have been more than a piece of traditionalism designed perhaps to ensure that the rest of his work would not be dismissed too summarily. But this does not appear to have been the case. Thistleton-Dyer (1893), in his obituary of de Candolle, suggests that it was partly the influence of ideas about the climatic factors of distribution and partly a somewhat unimaginative quality of mind that made him miss the essential point by so narrow a margin. How near he had been to it he himself fully realized later, and it is pleasant to notice in after correspondence Darwin's great opinion of the *Géographie Botanique Raisonnée* and his appreciation of its author's generous attitude toward his own theories.

Asa Gray's relation to the story of the *Origin* is different. He was one of the few confidants whom Darwin had kept informed of the gradual development of his own theoretical opinions about evolution. Indeed, one of his frequent letters to Gray, which happened to express some of his ideas particularly concisely and conveniently (as well as to date them), was included as part of the joint communication of Darwin and Wallace to the Linnean Society of London by which the theory of natural selection was launched on July 1, 1858. The exact relation of Gray's classic paper on the North American and Japanese floras to the *Origin* is not simple to gauge now. This relationship was the subject of correspondence between the two authors during the preparation of Darwin's great work for the press, and it seems fair to regard Gray's paper as having been written in a form intended to provide possible additional evidence for Darwin's views. On the other hand Gray's formal attitude toward these views of Darwin's was one of studied caution. Although Darwin considered Gray one of his most valuable supporters, this support was tempered by a certain criticism because, it would seem, Gray felt that a judicial attitude of this kind would be more effective aid in the long run than any more spectacular and enthusiastic championing.

Hooker's two great papers were rather more profound phytogeographical studies but are perhaps to be thought of as less intimately involved with the trend toward evolution. They were obviously of great importance to it, since the facts that they set forth spoke for themselvess in no uncertain voice. Of course Hooker was even more closely associated with Darwin than was Gray but, to use an apposite simile, the work of the two seems to illustrate convergence rather than strict homology. It is perhaps an interesting commentary on this point that Hooker, at any rate from 1850 to 1856, repeatedly expressed pessimistic opinions about the progress and future of botany as a science, which suggests that he was not altogether fully conscious of how rapidly the renaissance was approaching. Let us hope that some of the pessimisms of today are equally ill-founded.

However, we must not allow ourselves to wander farther down the by-ways of evolutionary history, fascinating though these are. What has been outlined has been intended to illustrate how opportune the founding of the Academy was and to call attention to the three great botanists, de Candolle, Gray, and Hooker, who dominated the phytogeographical scene at that time. There is nevertheless one other point about this birthday which must not be overlooked here, namely, that it occurred only three years after California had become a state of the Union. This surely is but further evidence, if such were needed, of that intellectual leaven to which reference has already been made.

With the coming of evolution the whole meaning of plant geography altered. It has often been said that the real evidence of the truth of the theory of evolution lies, not in this or that array of facts, but in its power as an organizing concept. Without it, the facts appear chaotic; with it, they fall into order to a remarkable degree. Nowhere is this more true than in plant geography, which is so fundamentally a mass of descriptive fact, and this is one of the reasons why it became to the evolutionists one of the most promising and popular aspects of botany. The other and even more important reason was the recognition, under the new conception, of the inevitable relation between time, space, and change. All this meant that the world vegetation and its distribution, which previously had been, as it has been expressed, matters for wonder but not for speculation, could now be, and indeed had to be, restudied from the point of view of the new theory, and a vast new field thus opened. Plant geography had, in short, to be translated into the new idiom. In this way the whole subject developed so quickly that only the most prominent features of its history can be noticed in one short paper.

It is very obvious from a study of botanical literature in general that the characteristics of different nations and peoples express themselves as much in their methods of scientific inquiry and in their predilection for certain aspects of their subjects as they do in many other ways. A philosopher could probably explain convincingly why it was that the German school of botanists almost at once made the newly opened fields so particularly their own, quickly reaching in them a preeminence which they maintained for many years. If an explanation is to be hazarded here, it is that this next phase of the subject was necessarily one of bringing some sort of order out of an enormous and rapidly accumulating mass of data, and that this was work which called for just those qualities of application, industry, and organization that are such strong German national features.

The first, and in some ways the greatest, of these German publications was Grisebach's *Vegetation der Erde* (1884), which first appeared in 1871, then in an enlarged edition in 1884. This may almost be described as the first full-scale attempt to give a coherent single description of the vegetation of the whole world and to classify it floristically, and the best compliment that can be paid it is to say that it is still an extremely valuable source of basic information. Indeed, the most striking thing about it now is how little it has been rendered obsolete by subsequent increase in our knowledge, and one can only be surprised that so authoritative and complete an account could be prepared at that comparatively early date. Actually, as the preface to the first edition says, the book is a synthesis of studies extending over thirty-five years, and thus is partly pre-Darwinian, as is evidenced by the stress laid on temperature as a distributional factor. This emphasis derives from de Candolle, and is partly Darwinian, as is shown by its clear expression of the evolutionary conception of adaptation to environment. It must also be borne in mind that this book dates from a time when the distinction between floristic and vegetational studies had scarcely begun to be made, and it would perhaps be fairer to regard it as an early essay in what later became distinguished as plant ecology (it contains, for instance, one of the first classifications of growth form), though it also includes much direct information about the spatial distribution of plants. A contemporary study more definitely developmental in outlook was the briefer early work of Engler which is often referred to as the *Versuch* (1872–1882).

The mention of Engler, who was, within the scope of his interests, one of the greatest of all German botanists, brings to mind another gradual divergence of subjects such as is inevitable with the passage of time and the growth of material. The study of plant geography must always rest largely on the devoted work of the taxonomists. In earlier days the two fields were almost parts of one whole, but later taxonomy came to absorb nearly all the energies of its chief practitioners. This is true of both Hooker and Engler, whose careers have many interesting parallels. Each was early attracted by geographical problems and retained his interest in these throughout his long life. But both later devoted themselves especially to systematics, Hooker's work in this field culminating (in collaboration with Bentham) in the *Genera Plantarum* (1862–1883) and in a number of floras, of which that of British India is preeminent (1875–1897), Engler's work in his well-known *Syllabus* (11th ed., 1936), and in the editing of such great undertakings as the *Natürlichen Pflanzenfamilien* (Engler and Prantl, 1889–1924) and *Das Pflanzenreich* (Engler, 1900). Much the same is true, too, of de Candolle, whose energies were later deeply absorbed in the continuance of his father's *Prodromus* (A. P. and A. L. P. P. de Candolle, 1824–1873).

Drude was perhaps in the more direct geographical succession, and in particular will always be remembered for his *Atlas der Pflanzenverbreitung.* This was published in 1887 as part of a larger physical atlas and consisted of a short series of excellently produced maps showing the ranges of various important plant elements, both vegetational and floristic, accompanied by a concise explanatory letterpress. The work of Drude, however, is more generally known from his *Handbuch der Pflanzengeographie,* which appeared in 1890 and contained among other things an improved floristic classification. This, however, though an important book, said little that was entirely new and gives the impression rather of belonging to the end of an epoch.

It is very noticeable, in the gradual development of a science, how often progress takes the form of successive pulsations, each giving great impetus to the study for a time but then tending to lose momentum, being replaced in due course by some new intensification along some rather different line. Thus it would seem that by the eighteen-nineties the forward urge provided by Darwinism had begun to work itself out and that some new impulse was due. This came in the form of a concentration upon the relation between the plant and its immediate environment or habitat, a new approach or point of view to which was given the name "plant ecology," or "oecology," as it was first spelled. The first principles of this new discipline, which, as we shall see, has since become the sister of the older plant geography in the stricter sense, were set forth in two books which were, effectively, more or less contemporaneous. These were Warming's *Plantesamfund,* published in Denmark in 1895 and later translated into the more familiar *Oecology of Plants,* and Schimper's *Pflanzen-Geographie auf Physiologische Grundlage* (1898), which also was translated into English some years later.

There is no doubt that a powerful influence in the hiving off of plant ecology was the reaction against the aridity which had affected much of botany through an overemphasis on formal morphology. It may be said to have been based on two fundamental propositions: that the plant itself is a living organism in close and intimate relation, both functionally and structurally, with the conditions of its environment, and that vegetation is a dynamic complex expressing the same laws of universal change with time as everything else in nature. Schimper himself expressed this idea (loc. cit.) when he said that the problems of plant geography will not be exhausted when the world flora is completely known (a contingency which, strangely enough, he seems to have thought imminent) but will become of a rather different sort and particularly concerned with the explanations of the differences between floras in different parts of the world.

For vegetation is always developing; floras occupy only a moment of vegetational history; and it is the relation of structure, function, and environment which must be studied.

It was very early recognized that plant geography is a matter which involves, in a peculiarly direct way, the fundamental conceptions of both space and time, and that the subject might, therefore, be approached from one or other of these directions or from some combination of both. Thus there has always been in plant geography an underlying triplicity; the swing of emphasis within this provides the background to the history of the subject. Just how the three streams or branches of plant geography should be defined and named has been a matter of considerable argument. Those who are interested in terminologies will find excellent accounts of this by Rübel (1927) and by Wulff (1943), but it is more convenient here to describe this triplicity in rather freer terms. First, there is the stream in which the main emphasis is the correlation of space and form; this has been the special concern of those plant geographers, like de Candolle, Hooker, Asa Gray, and Engler, who have also been preeminent systematists. It may be called the taxonomic stream. Second, there is the stream in which the strongest emphasis is placed upon the historical and developmental aspects of the subject, and this is perhaps most often now called the historical stream. Third, there is the stream in which the two conceptions of space and time are balanced more evenly than in either of the others, namely ecology, which is mainly concerned with the distributional changes, usually by their nature relatively small, resulting from the gradual changes in a mutable environment.

The main point in relation to this analysis is very clear: the coming of Darwinism shifted the emphasis away from the first stream, where it had in fact been almost wholly concentrated, and distributed it more evenly among all three. For a good many years the full effect of this was not felt because this was a period of reorientation, but once this adjustment had been made, the rapid development of the streams which had been so long held back by the pre-evolutionary conception of the cosmas was inevitable. For reasons which we need not attempt to specify too closely but which are certainly connected with the full flowering of the idea of adaptation to environment the ecological stream was the first to break through.

So simple an analysis is likely to be too clear-cut to depict the whole truth, and this is certainly so here, especially with regard to the first two streams, between which there has always been a close connection. We may indeed recognize two streams, but there is, as it were, a constant interchange of water between them. The ecological stream, however, has much more noticeably scoured its own channel and, although this stream flows alongside the others, there is little actual communication between them. The reasons for this would make a most interesting study, for they are probably not all purely botanical, but this is no place to attempt it. We must content ourselves with the statement that what is now called plant ecology became in a comparatively short time largely divorced from the other aspects of plant geography. There is therefore both reason and excuse for referring only briefly to it here, apart from the fact that, since ecology was unknown as a separate study in 1853, it may formally be considered outside the terms of present reference.

It is difficult to mark the exact point at which plant ecology became established as a separate subject, but it is not unreasonable to think of Schimper's *Pflanzen-Geographie* as belonging to the older dispensation and of Warming's *Plantesamfund* as belonging to the new, though in fact this is the reverse of their actual dates of appearance. Apart from these two it was perhaps the work of Flahault, of Montpellier, rather than that of any other man that gave the initial impulse to ecology, which at first consisted largely of the mapping of vegetation, such as he had been doing in France for some years. At all events it was one of his pupils, Robert Smith, who introduced his methods into Britain. But shortly after this Smith unfortunately died and, although his work was carried on by his brother and others, it later met with practical difficulties. Attention then passed, largely under the leadership of Tansley, happily still with us, rather to the analysis of vegetation and the study of the different kinds of plant communities, work in which a very definite stage was reached by the publication in 1911 of Tansley's *Types of British Vegetation.*

As might be assumed, a similar and indeed even greater development had been taking place synchronously on the continent of Europe, in which indeed so many names claim recognition that it is almost invidious to make a selection. Among the significant works the following stand out clearly: Schröter's publication (with Früh) of *Die Moore der Schweiz* (1904), which was a landmark; Raunkiär's classic study of growth form (1907); and Rübel's later work, *Pflanzengesellschaften der Erde* (1930), which is a remarkable study of European plant communities. According to Tansley (1911) Schröter also deserves mention as the first to distinguish between "synecology," or the study of plant communities in relation to their habitats, and "autecology," or the study of the ecology of single species.

In America the growth of the new subject went hand in hand with that in the Old World, as instanced by Hitchcock's *Oecological Plant Geography of Kansas* (1898) and by the *Phytogeography of Nebraska* by Pounds and Clements (1900), but with a rather greater emphasis on the developmental aspects. By 1899 Cowles had begun to publish on the subject of plant succession, the great later expansion of which under the leadership of Clements (1916) is one of the notable features of American plant ecology. It is interesting to note this difference of emphasis for it is surely indicative of the great distinction between European and American ecological development. European botanists had, of necessity, to work upon a vegetation which could be considered natural only by a considerable exercise of imagination, whereas the American school had as its subject vast areas of country over which the influence of man had scarcely been felt at all. It is not surprising in this circumstance that American ecology developed very rapidly and, in many directions, soon attained a leading position.

Although it has been convenient to regard plant ecology as stemming from Schimper and Warming, it needs to be stressed that this really marks the formal separation of the subject—its coming of age—rather than its birth, for these were certainly not the first publications written from the ecological standpoint. There were, for instance, the studies of Graebner (1895) and others on the North German heaths in the earlier 'nineties; and, especially, Drude's account in 1890 of the plant formations of Central Europe, which actually incorporated some forms of later ecological nomenclature. Earlier still, in the 'eighties, there were Krasnov's account of some of the Russian steppes (1886), Sargent's report on the North American forests (1884), and Christ's book on the Swiss vegetation (1879). Indeed, from almost the earliest days there had been a slowly increasing concern with ecological problems in plant geography, until shortly before the first World War the literature of ecology had grown so great that it became desirable to establish special periodicals to accommodate it, a stage it which we may perhaps consider the subject to have passed, for the time being at least, beyond the purview of this paper.

The end of the nineteenth century marked also the centenary of the departure of von Humboldt and Bonpland on their travels in tropical America. Readers will find an interesting account of the development of plant geography up to 1900 in Engler's contribution to the Centenary volume of the Berlin Geographical Society (1899), in which he first traces the beginnings of the subject from the earliest times and then its gradual growth on the floristic side, region by region.

The double deflection, or apparent deflection, of interest which followed the turn of the century, on the one hand toward more narrowly taxonomic work and on the other toward ecology, for a time left the middle stream of plant geography a somewhat feeble one. In this direction, at any rate, the fifteen years or so preceding the war were not among the most remarkable. This diversionary tendency was intensified also by one of the most considerable advances of that time, the growth of the subject of genetics, for, as will be seen, it was not until considerably later that the underlying unity between genetics and plant geography became perfectly realized.

Nevertheless these years were far from being entirely barren. In particular the German school continued to demonstrate its leadership in its chosen fields by the continuation or launching of such great projects as Engler and Drude's *Die Vegetation der Erde* (1896—)—among the volumes of which Harshberger's *Phytographical Survey of North America* is conspicuous—and Karsten and Schenk's *Vegetationsbilder* (1903—) which presents so much of interest and importance in the international language of illustration; by such books as those of Solms-Laubach (1905) and Schröter (1912); and by innumerable shorter publications, notably in Engler's *Botanische Jahrbücher*. Most of these are on the border line between historical and taxonomic plant geography, but an important direct contribution to the former was the comparison by Engler of the floras of tropical Africa and of tropical America, a subject which was later to become much more topical.

In addition, these years saw the earlier writings of several whose major contributions to plant geography were to come after the war, among them Fernald, Merrill, Skottsberg, and Willis, but one of the most important series of writings came from H. B. Guppy. Guppy was not a biologist by professional training except in so far as he began his career as a naval surgeon, but he was that much rarer thing, a born naturalist and observer, and he made good use of the fortune which took him for many years to what are some of the most interesting parts of the world from the point of view of plant geography. His larger works, namely, *Observations of a Naturalist in the Pacific* (1903–1906), *Studies in Seeds and Fruits* (1912), and *Plants, Seeds and Currents in the West Indies and the Azores* (1917), are perhaps a little voluminous and prolix for ordinary reading but they are unquestionably the work of a mind possessed of unusual descriptive and analytical powers. The second volume of the first-mentioned work, which deals with plant dispersal, will long remain a classic source of fact and commentary on that subject and its many related problems. Rather later on, and partly in association with Willis, Guppy turned his attention toward historical plant geography, and two of his papers in this field, *The Island and the Continent* (1919), and *Plant Distribution from the Standpoint of an Idealist* (1917–1920), are notable for their penetration and freshness of thought.

Again, although the prewar years may not have been very eventful scientifically, it was in this period that the foundations were laid for much of the later progress, especially in the increase of knowledge during the years in two fields relating to the distant past. First, it was a time of great activity in paleobotany, and although the more spectacular expressions of this centered in epochs too remote to interest the phanerogamist, it produced many important studies on fossil angiosperms. Among these the earlier works of Berry in America (e.g., 1911) and the studies of the Reids in England (e.g., 1908) may be specially noted, the one adding to our knowledge at the earlier end of the angiosperm time scale, the other at the later end. Second, there was a great development in the study of glaciation and its possible consequences, particularly as regards the Pleistocene. It may be claimed that our modern conceptions on this subject date from these years, which saw the publication of Penck and Brückner's *Die Alpen in Eiszeitalter* (1901–1909), as well as much of the work of Andersson, de Geer, and others.

This is perhaps the most appropriate point also for a brief reference to the study of the distribution of cryptogamic plant groups. Because the spermatophytes reproduce by what are usually macroscopic seeds, because they generally have bulky and resistant plant bodies, and because they have a relatively short geological history, their plant geography has particular values of its own which must not be applied to other groups, though each group has its own relation to this subject. Unfortunately, for the lower plants, much less of the necessary background knowledge is available and the practical difficulties are greater; thus it is fair to say that the only groups of cryptogams which have received the same kind of geographical treatment as the seed plants are the easily collected groups of the ferns and mosses. Christ's standard work on ferns, the *Geographie der Farne* (1910) dates from these prewar years, but the main work of this period, Herzog's *Geographie der Moose,* was rather later (1926). Most groups have of course received incidental treatment in the course of taxonomic studies, as for instance in the two editions of the *Pflanzenfamilien,* but, apart from those mentioned, the only plants which need comment are the lichens, another easily collected group, some of which have long attracted attention by reason of their extraordinarily wide ranges. Indeed, crytogamic phytogeography is largely an untilled field, but it is also one with special difficulties of its own, chiefly inherent in the much longer and more hazy geological history of these plants.

About the time of the first World War another switch of emphasis became apparent. As already explained, Schimper had long since pointed out that existing floras exhibit only one moment in the history of the earth's vegetation and that in consequence the history of the earth's surface is a matter which must deeply concern the plant geographer. About 1915 several circumstances conspired to focus attention on this aspect of the subject, so that what had in fact always been its core became crystallized more definitely than hitherto into what has now become known as historical plant geography. Among these circumstances was certainly the normal swing of the pendulum, in this case from the extreme of formal taxonomy and purely descriptive ecology. Two other not clearly related influences, however, were more particularly concerned. These were the publication by Willis (1922) of his theory of age and area and the publication by Wegener (1924) of his theory of continental displacement.

There is much evidence for the belief that the success of a scientific theory has often been due to the fact that a general combination of trends and circumstances, not in themselves easily discernible, have served to predispose public opinion favorably toward it, almost as if an unconscious sort of propaganda had been at work. There is little doubt, for instance, that this is broadly true of Darwinism itself, which, when the time was fully ripe, became widely established with what was really remarkable rapidity and unanimity. So with the two theories just mentioned. They were something new when the times were set for novelty and because of this, and also perhaps because each contained an element of the mysterious, they gained considerable attention.

Willis' work appeared straightforwardly as a contribution to botanical thought, but it developed from an evolutionary approach to the subject. Readers may find elsewhere (e.g., New Phytol. [1951], 50: 135) accounts of it longer than is appropriate here. It need only be said that Willis was attracted to the subject of plant geography mainly because of the way in which it seemed to him capable of helping toward a better understanding of the processes of organic evolution and particularly because of the way it might be made to afford evidence against the theory of natural selection, which Willis' experience caused him to criticize. Very briefly, Willis maintained that the choice lay between natural selection and mutation and that, since mutation requires no assumption of a widespread supersession and elimination of "unfit" species, which is inherent in the conception of natural selection, any detection of an exponential rate of speciation and spread might be held to indicate that mutation rather than selection had been the paramount process in evolution. Such an exponential rate Willis claimed to demonstrate in the "hollow curve" type of graph. As a projection of this, as it were, Willis argued that under continuous mutation, not only would the totality of species constantly increase, but, barring accidents, the longer a species existed the wider would be its spread, and it is by this conception of "age and area," as he called it, that his scientific work is most familiar.

This is not the place to attempt an appraisal of Willis' theories or an assessment of his direct contribution to plant geography as such. His claim to a place in the history of that subject is based on something rather different, for the service that he rendered was that of provoking (to use the *mot juste*) a renewed interest in the whole science. But this does not altogether explain the almost violent reaction that many of his opinions occasioned and there were, it seems, two other reasons. One certainly was that he had the temerity to question the long popular theory of natural selection; the other, that he puts into words what many felt. For both these different reasons his writings received a measure of publicity and criticism which possibly surprised no one more than their author.

As we now look back through the years, the nature of Willis' achievement in plant geography has become clearer. It is that he showed, even if without first intent, that plant geography was not the exhausted subject which had yielded place to more modern disciplines but was a living one which still posed profound problems of fundamental importance. In short, he did much to restore to it the prestige which, during the previous generation, it had seemed to lose; and it is important to realize this because it helps to relate his work to that which we must now go on to notice.

Wegener's theory of continental displacement, or "drift" as it is sometimes called, dates from about 1915, though it did not become common currency until after the war, and its basic conception was not altogether novel. The relation between ideas of continental displacement and plant geography is a double one. First, the facts of discontinuity or disjunction, using those terms in their widest sense, clearly provide some circumstantial evidence for or against the view that displacement may have occurred; second, the idea is valuable to those who would explain the floristic relationships which today exist between the separate continental masses. Both aspects combine to make drift a particularly live problem for plant geographers.

Up to the present, and despite an enormous amount of study from various points of view, ideas of continental movement remain hypothetical. No summing up of the matter is really possible, but the situation in relation to the geography of the flowering plants, as it stands today, can be stated quite shortly. For at least one hundred years—which means in effect ever since the subject of plant geography took real form—there has been a common belief that the leading facts cannot be explained at all satisfactorily so long as it is held that the geography of the world, and particularly the isolation of the continents, has always been as it is now. In this connection it is well to remember that there are two ways in which a junction may be effected between separated entities. One is by interposing something in such manner as to bridge the gap between them; the other is by moving one or other of them bodily until the two come into contact. The first method, since it did no violence to generally accepted beliefs, was for long the accepted explanation; but it has aspects which, purely from the point of view of the plant geographer, make it a less attractive proposition than the second. As for the more direct geological and other evidences for displacement, these are at present generally held to be inadequate, and those who favor this theory are therefore faced with the fact that, on this ground, it is not generally acceptable to geologists and geodesists. How far this essentially negative attitude of objection is justified time alone will show; but there are not a few who feel that the rejection of a hypothesis simply on the ground of inexplicability is unwise. Finally, with regard to Wegener's theory it must not be forgotten that it involved not only continental displacement, but also the idea of a more or less continuous movement of the poles. Any such movement would of course in turn involve corresponding movements in the climatic zones of the world, and a possibility of this kind as an explanation of many difficult phytogeographical facts has scarcely been sufficiently examined as yet.

Early in the interwar years there came two important developments which derived directly from the earlier work on glaciation already mentioned. The more important was the growth, under the leadership of Erdtman (1943) and others, of the technique of pollen analysis. This technique made it possible to form various postulates from the proportionate occurrence of different kinds of pollen grains in peat and similar deposits about the nature of the vegetation contemporary with the deposits and thus to draw a much more complete picture of the general conditions of the time. Strictly, pollen analysis is on the borders of plant geography, especially where that subject impinges on archaeology, but within its limitations it has been and doubtless will continue to be a valuable adjunct.

The second development was the discussion which grew up around what is usually called the "nunatak theory," the view that some elements of the preglacial floras survived those ages on refuges actually within the ice-cap but not themselves glaciated. This idea again was not in itself new, but in the nineteen-twenties it received much fresh impetus from the explorations of Fernald in the region of the St. Lawrence River, and from his energetic writings (e.g., 1925). The general suggestion of which this was a particular expression is an attractive one, namely, that the explanation of certain puzzling phytogeographical facts is to be found in the occurrence of refuges where plants may have been able to avoid the worst consequences of climatic change and survive. But there is as yet no overwhelming evidence that it is necessary to invoke this explanation.

The last few paragraphs deal with matters which, despite their apparent diversity, nevertheless have a considerable common element, revealing clearly the main trend in the study of plant geography between the two wars, namely, its concentration on the historical-developmental aspects of the subject. Major works in this tradition soon appeared, and price of place may be given to Irmscher's *Pflanzenverbreitung und Entwicklung der Kontinente,* published in 1922 and followed in 1926 by Hayek's *Allgemeine Pflanzengeographie,* which, although much more of a textbook, had the same approach. Both of these are important, but it is fair to regard a later book as the real primer of the new interest. This was Wulff's *An Introduction to Historical Plant Geography* (1943), which was composed much more in the new idiom than either of the earlier books. This publication is important, too, as marking the entry into the field of the great new Russian school of botanists which had grown up since the Revolution, a school whose full influence is still impeded by barriers of alphabet and language. Fortunately Wulff's first volume, which was published in 1932, was translated into English during the war, but his second and much larger volume is still available only in Russian. This is also true of the monumental *Flora URSS* edited by Komarov, begun in 1934 and still in active progress. It contains a great mass of information about the distribution of plants over the huge but hitherto little studied tracts of much of central and eastern Asia.

This is perhaps the best place at which, ignoring chronology for the moment, to refer briefly to two later publications, because, with that of Wulff, just mentioned, they form a mutually complementary trilogy, covering with reasonable adequacy most aspects of modern plant geography and giving as complete a picture of the present situation as can, in all circumstances, be expected. These are Cain's *Foundations of Plant Geography,* which appeared in 1944, and the present writer's book, *The Geography of the Flowering Plants,* written before the late war but unavoidably delayed in production until 1947. Both have historical plant geography as their chief emphasis, but while the former is of special interest for its treatment of many particular aspects of the relation between evolution and plant geography, such as polyploidy, the latter is rather more a review of the facts of angiosperm distribution and a reconsideration, from a developmental point of view, of the factors which have caused them. All three of these books take, at least as a partial basis, the theory of tolerance, published in 1931, by the author of the last of them in an attempt to integrate into some generally applicable working hypothesis of plant geography the many "factors of distribution."

Returning now to a more general consideration of the interwar years we find that the literature of plant geography is so extensive that it is difficult to select from it, though several broad features demand comment. One of these is the special attention given, notably by German workers, to the more detailed study and analysis of types of distribution area, or areography as it has come to be called, a subject to which Hannig and Winkler's new serial publication *Die Pflanzenareale,* founded in 1926, contributed much and of which there have been various minor reflections in more recent years. Another noteworthy and valuable feature of this period was the large number of memoirs written about various phytogeographically strategic parts of the world by authors fully conversant with their floras. Anything like an exhaustive list would be much too long here, but they may be exemplified by the work of several authors: Allan and Oliver for New Zealand; Bews for South Africa; Perrier de la Bathie for Madagascar; Gleason for the mountains of southern Venezuela; Guillaumin and others for New Caledonia; Setchell and many others for various parts of the Pacific; Scottsberg and St. John for Hawaii; Skottsberg for Juan Fernandez; Lam and van Steenis for parts of Malaysia; Merrill for the Philippines, and Hultén for the region of the Bering Strait.

With all this went many advances in cognate subjects, as, for instance, the study of angiosperm fossil floras in which the work of Berry and, rather later, Chaney was notable, but for the rest it must suffice to mention, as representative of many others, three books which, though very different from one another, nevertheless each added something of worth to the general store. The first of these, in order of appearance, was Marcel Hardy's little book *The Geography of Plants* (1925), the uninspired title of which may well have served to obscure its very real merit as one of the few really concise and readable general accounts of world vegetation as a whole. The second is the volume of essays published in honor of W. A. Setchell (Goodspeed, ed., 1930) in which a number of eminent phytogeographers give authoritative accounts of their own special interests. The third is Ridley's great book *The Dispersal of Plants Throughout the World* (1930), in which there is surely gathered together all that is known, or at least was known at that time, about this peculiarly bewildering subject. Probably no other branch of plant geography has been so misunderstood, and even so much misrepresented, as this, and Ridley, although he confines himself largely to the recording of facts, at least provides some kind of sheet anchor, so that the subject may be more safely approached.

Of the years since the outbreak of the second World War not much can be said here. They are too close to allow us to generalize and it can only be said that the literature is still copious and shows no sign of abatement. One or two items of this period have already been referred to and to these a few others must be added. Two publications of the actual war years testify to the continued vitality of what has been called here the German school, namely, three papers by Vester (e.g., 1940), in which he summarizes, with the help of small maps, the distributions of all the families of angiosperms, and Meusel's book *Vergleichende*

Arealkunde (1943), which is in many respects a textbook of areography. More recent is the great Dutch project of the *Flora Malesiana* (van Steenis, ed., 1948—), which, although in the main taxonomic, is so broadly based on geographical principles that it can scarcely fail to add enormously to our knowledge of the distribution of plants in a particularly significant part of the world. There are also numerous accounts of the phytogeography of sundry parts of the northern temperate regions and to represent these there can be no better choice than Hultén's beautifully produced *Atlas* (1950), which deals exhaustively with the geography of the Scandinavian flora. Of very different scope is Willis' third and largest book *The Birth and Spread of Plants* (1949) which, somewhat hidden by a rather awkward kind of presentation, contains much of real importance.

The war itself was responsible for not a little progress in the paths of plant geography. The extension of hostilities into the great and relatively unfamiliar spaces of the Pacific, especially, caused a considerable revision and augmentation of our knowledge of those regions, in which the botanists took their fair share, as is instanced by Merrill's useful and delightful account (1946) of tropical vegetation in that area.

But the over-all impression of these later years, and one indeed hopes that it is a true estimate, is that there is coming about a much needed reintegration of the different branches of plant geography. This may be illustrated by reference to three points. First there is the growing tendency for purely taxonomic works, such as floras and systematic monographs, to pay more attention to the geography of their subjects, to bring together as much geographical information as they are able to and often to illustrate it with maps. This is desirable enough in itself, but it is also an enormous help to the phytogeographer, who must rely so much on reliable taxonomy for the facts which he endeavors to interpret. Second, one has only to look at recent volumes of the periodicals devoted to ecology to see how much the horizons of the ecologists have widened and how much more concerned with the main stream of plant geography they are becoming. Finally, there is the development which, more than anything else perhaps, characterizes the postwar years, namely, the growth of that combination of taxonomy, geography, and genetics which has come to be known as cytogeography, itself so essentially a synthetic effect. It is very apposite, in this volume which celebrates the first hundred years of the California Academy of Sciences, to mention a publication which best typifies this latest phase in the development of plant geography, Babcock's great study of the genus *Crepis,* which appeared in 1947. It is further work of this kind, based on phytogeographically significant plant groups, that is more likely than almost anything else to speed the progress of plant geography.

At the end of the first century of the Academy's history, what are the chief impressions? Two seem particularly noteworthy. One is the truth of the aphorism, *Plus ça change, plus c'est le même chose.* Probably no previous hundred years has seen such profound changes as this latest century, certainly not in the scientific world, and yet one cannot help feeling that, if Alphonse de Candolle and some of the other pioneers of plant geography could once more walk the earth, they would understand us and our problems pretty well, though we might for a time speak in rather different dialects. Advance in knowledge since their time has indeed been enormous, but it has been amplification rather than violent change, evolution rather than revolution. There have been secessions, but there have also been federations, and the main outlines of the subject now are very much what they were a hundred years ago. The difference is that we have a deeper understanding of them.

A second impression, or so it seems to the present writer, is that today, just as in 1853, we stand on the threshold of great advances in biological thought and method. Our particular subject, plant geography, involves the former rather than the latter, but the indications of future change are not far to seek. There is an increasing impatience with ideas which owe their perpetuation more to tradition than to logic, and for many there is a growing doubt of our ability to arrive at the answers of some of our most urgent problems with our present major postulates. It is easy enough, one realizes, to forecast change when there is no obligation to foretell its shape, but its prognostication may at least help us to be ready for it and to take advantage of it.

To this end there are two aids. The first is austerity, or perhaps asceticism is a better word, in scientific thought and theory. Today the pressure of events and many other influences combine to make more than ever difficult the pursuit of truth for its own sake, and it must not be forgotten that this is the only real road to scientific progress. There is need too for a higher standard of logical argument and a stronger guard against facile generalizations and false conclusions. The second requisite is receptiveness and suppleness of mind which, it is perhaps worth stressing, is in no way antipathetic to intellectual integrity. Every new idea, however fantastic it may appear at first sight, is entitled to critical consideration, and the wise man will treat none with complete contempt. It has been well said that all great truths begin as heresies and that all new knowledge contradicts the old. However true this dictum may or may not be, it is at any rate an admirable motto for the study wall of the plant geographer.

BIBLIOGRAPHY

Babcock, E. B.

1947. The Genus *Crepis*. Pt. I. The Taxonomy, Phylogeny, Distribution, and Evolution of *Crepis*. Univ. Calif. Publ. Bot., 21. xii + 197 pp. Berkeley and Los Angeles.

Bentham, G., and J. D. Hooker

1862–1883. Genera Plantarum. 1(1862–1867); 2(1873–1876); 3(1883). London: Reeve and Co.

Berry, E. W.

1911. The Lower Cretaceous Flora of the World. *In* Maryland Geol. Surv., 1896—Cretaceous . . . 1911, pp. 99–151.

Cain, S. A.

1944. Foundations of plant geography. 556 pp. New York: Harper.

Candolle, A. L. P. P. de

1855. Géographie Botanique Raisonnée. Vol. I, xxxii + 606 pp.; Vol. II, 607–1365 pp. Paris: V. Masson.

Candolle, A. P. and A. L. P. P. de

1824–1873. Prodomus Systematis Naturalis Regni Vegetabilis. 17 vols. Paris: Treutel et Würtz.

CHRIST, H.

1879. Das Pflanzenleben der Schweiz. xiv + 488 pp. Zürich: F. Schulthess.

1910. Die Geographie der Farne. 357 pp. Jena: G. Fischer.

CLEMENTS, F. E.

1916. Plant Succession. Carnegie Inst. Wash. Publ. No. 242. 512 pp. Washington.

COWLES, H. C.

1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz., 27:95–116, 167–202, 281–308, 361–391.

DARWIN, CHARLES

1859. The Origin of Species by Means of Natural Selection. 6th ed., 1881. 434 pp. London: Watts.

DRUDE, O.

1887. Atlas der Pflanzenverbreitung. 6 pp., 8 maps. Gotha: J. Perthes.

1890a. Handbuch der Pflanzengeographie. 582 pp. Stuttgart: J. Engelhorn.

1890b. Vegetationsformationen erläutert an der centraleuropäischen Flora. Bot. Jahrb. Engler, 11:21–51.

ENGLER, A.

1879–1882. Versuch einer Entwickelungsgeschichte der Pflanzenwelt. I, 202 pp.; II, 347 pp. Leipzig: Engelmann.

1899. Die Entwickelung der Pflanzengeographie in den letzten hundert Jahren und weitere Aufgaben derselben. *In* Wiss. Beitr. z. Gedächtniss der hundertjährigen Wiederkehr des Antritts v. A. v. Humboldt's Reise nach Amerika, 1799. Ges. Erdkunde. 247 pp. Berlin: W. H. Kühl.

1900– (Ed.) Das Pflanzenreich. 105 vols. Leipzig: W. Engelmann.

1905. Ueber floristische Verwandschaft zwischen dem tropischen Afrika und Amerika, sowie über die Annahme eines versunkenen brasilianisch-Äthiopischen Continents. Sitzungsber. K. Preuss. Akad. Wissen. Berlin, 1905(6):180–231.

ENGLER, A., and O. DRUDE (eds.)

1896–1928. Die Vegetation der Erde. 1st and 2d eds. 15 vols. Leipzig: W. Engelmann.

ENGLER, A., and L. DIELS

1936. A. Engler's Syllabus der Pflanzenfamilien. 11th ed. xiii + 419 pp., 476 figs. Berlin: Gebr. Borntraeger.

ENGLER, A., and K. PRANTL

1889–1924. Die natürlichen Pflanzenfamilien. 1st ed., 1889–1915; 2d ed., 1924– . Leipzig: W. Engelmann.

ERDTMAN, G.

1943. An Introduction to Pollen Analysis. 239 pp. Waltham, Mass.: Chronica Botanica.

FERNALD, M. L.

1925. Persistence of plants in unglaciated areas of boreal America. Amer. Acad. Arts and Sci. Mem., 15:241–342.

GOOD, R.

1931. A theory of plant geography. New Phytol., 30:149–171.

1947. The Geography of the Flowering Plants. 403 pp. London and New York: Longmans, Green.

GOODSPEED, T. H. (ed.)

1936. Essays in Geobotany in Honor of William Albert Setchell. xxvi + 320 pp. Berkeley: Univ. Calif. Press.

GRAEBNER, P.

1895. Studien über die norddeutsche Heide. Bot. Jahrb. Engler, 20:500–654.

GRAY, A.

1859. Diagnostic characters of new species of phaenogamous plants, collected in Japan by Charles Wright, with observations upon the relationship of Japanese flora to that of North America, and other parts of the north temperate zone. Amer. Acad. Arts and Sci. Mem., n.s., 6:377–452.

GRISEBACH, A. H. R.

1884–1885. Die Vegetation der Erde nach ihrer klimatischen Anordnung. 2d ed. Vol. 1, 567 pp.; Vol. 2, 594 pp. Leipzig: W. Engelmann.

GUPPY, H. B.

1903–1906. Observations of a Naturalist in the Pacific between 1896 and 1899. Vol. 1 (1903), Vanua Levu, Fiji, xix + 392 pp.; Vol. 2, Plant Dispersal, xxvi + 627 pp., 5 pls., 5 maps. London and New York: Macmillan.

1912. Studies in Seeds and Fruits. 528 pp. London: Williams and Norgate.

1917. Plants, Seeds and Currents in the West Indies and the Azores. 531 pp. London: Williams and Norgate.

1917–1920. Plant distribution from the standpoint of an idealist. Journ. Linn. Soc. Bot., London, 44:439–471.

1919. The island and the continent. Journ. Ecol., 7:1–4.

HANNIG, E., and H. WINKLER (eds.)

1926– Die Pflanzenareale. 5 vols., Vol. 2 with L. Diels; Vol. 3 with G. Samuelsson; Vol. 5, maps. Jena: G. Fischer.

HARDY, M.

1920. The Geography of Plants. 327 pp. Oxford: Clarendon Press.

HARSHBERGER, J. W.

1911. Phytogeographical Survey of North America. lxiii + 790 pp. New York: Stechert and Company.

HAYEK, A.

1926. Allgemeine Pflanzengeographie. 409 pp. Berlin: Gebr. Borntraeger.

HERZOG, T.

1926. Geographie der Moose. 439 pp. Jena: G. Fischer.

HITCHCOCK, A. S.

1898. Oecological plant geography of Kansas. Acad. Sci. St. Louis. Trans., 8:55–69.

HOOKER, J. D.

1853. Introductory Essay to the Flora of New Zealand. London.

1859. On the Flora of Australia, its Origin, Affinities and Distribution; being an Introductory Essay to the Flora of Tasmania. 128 pp. London: L. Reeve.

1875–1897. The Flora of British India. 7 vols., in 24 parts (1872–1897). London: Reeve and Co.

HULTÉN, E.

1950. Atlas över Växternas Utbredning i Fanerogamer och Ormbeinksväxter Norden. 512 pp. Stockholm: Generalstabens.

HUMBOLDT, A. VON

1817. De Distributione Geographica Plantarum, Secundum Coeli Temperiem et Altitudinem Montium Prolegomena. 249 pp. Paris.

IRMSCHER, E.

1922. Pflanzenverbreitung und Entwickelung der Kontinente. Studien zur genetischen Pflanzengeographie. Hamburg Inst. Allgem. Bot. Mitteil., 5:17–235.

KARSTEN, G., and H. SCHENK (eds.)

1904–1944. Vegetationsbilder. 26 vols. Jena: G. Fischer.

KOMAROV, V. L. (ed.)

1934–1952. Flora URSS. 18 vols. Moscow and Leningrad: The URSS Acad. Sci. Press.

1941. Materials on the History of the Flora and Vegetation of the URSS. Fàsc. I. 413 pp. Moscow and Leningrad: The URSS Acad. Sci. Press. (English summaries of Russian papers.)

KRASNOV, A.

1886. Geobotanical researches in the Kalmuk steppe. Russ. Geog. Soc. St. Petersb. Bull., 22:1–52.

MERRILL, E. D.

1946. Plant Life of the Pacific World. 295 pp. New York: Macmillan.

MEUSEL, H.

1943. Vergleichende Arealkunde. 2 vols., Vol. 1, 437 pp. Berlin: Gebr. Borntraeger.

PENCK, A., and E. BRÜCKNER

1901–1909. Die Alpen in Eiszeitalter. 3 vols. Leipzig: C. H. Tauchnitz.

POUND, R., and F. E. CLEMENTS

1900. The Phytogeography of Nebraska. 442 pp. 2d ed. University of Nebraska.

RAUNKIÄR, C.

1907. Planterigets Livsformer og deres Betydning for Geografien. 132 pp. Copenhagen.

REID, C., and E. M. REID

1908. On the pre-glacial flora of Britain. Journ. Linn. Soc. Bot., London, 38:206–227.

RIDLEY, H. N.

1930. The Dispersal of Plants throughout the World. 744 pp. Ashford, England.

RÜBEL, E.

1927. Ecology, plant geography and geobotany, their history and aim. Bot. Gaz., 84:428–439.

1930. Pflanzengesellschaften der Erde. 464 pp. Bern-Berlin.

SARGENT, C. S.

1884. Report on the forests of North America. 612 pp. Washington: Government Printing Office.

SCHIMPER, A. F. W.

1898. Pflanzen-Geographie auf physiologische Grundlage. (1903) 876 pp. (Eng. trans. by Groom and Balfour, 1903. Oxford.) Jena: G. Fischer.

SCHRÖTER, C.

1912. Genetische Pflanzengeographie. Jena.

SCHRÖTER, C., and J. FRÜH

1904. Die Moose der Schweiz. Berne.

SOLMS-LAUBACH, H.

1905. Die leitenden Gesichtspunkte einer allgemeinen Pflanzengeographie in kurzen Dorstellung. 243 pp. Leipzig: A. Fèlix.

STEENIS, C. G. G. J. VAN (ed.)

1950– Flora Malesiana. Djakarta: Noordhoff-Kolff.

TANSLEY, A. G.

1911. (Ed.) Types of British Vegetation. xx + 416 pp. Cambridge Univ. Press.

1947. The early history of modern plant ecology in Britain. Journ. Ecol., 35:130–137.

THISTELTON-DYER, W. T.

1893. Alphonse de Candolle. Nature, 48:269–271.

VESTER, H.

1940. Die Areale und Arealtypen der Angiospermen-Familien. Bot. Archiv, 41:203–275, 92 figs.

WARMING, J. E. B.

1895. Plantesamfund. vii + 335 pp. Copenhagen: P. G. Philipsen.

WEGENER, A. L.

1924. The Origin of Continents and Oceans. (Eng. trans. from 3rd German ed. by J. G. A. Skerle.) xx + 212 pp. London: Methuen Co.

WILLIS, J. C.

1922. Age and Area. A Study in Geographical Distribution and Origin of Species. 259 pp. Cambridge: Univ. Press.

1949. The Birth and Spread of Plants. Geneva.

WULFF, E. V.

1943. An Introduction to Historical Plant Geography. (Eng. trans. by E. Brissenden.) 223 pp. Waltham, Mass., U. S. A.